From: Martin Nowak <[redacted]>
To: Jeffrey Epstein <jeevacation@gmail.com>
Subject: Fwd: Inclusive Fitness & Eusociality
Date: Tue, 07 Sep 2010 15:30:19 +0000

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127. einstein only got 100.

Bring me my bow of burning gold
Bring me my arrows of desire
Bring me my spear - oh clouds unfold
Bring me my chariot of fire

Begin forwarded message:

From: Stu West <[redacted]>
Date: September 7, 2010 10:01:50 AM EDT
To: [redacted]
Subject: Inclusive Fitness & Eusociality

Dear Professor's Nowak/Tarnita/Wilson,

A couple of us have been puzzled by some of the statements on inclusive fitness and eusociality in your recent Analysis, as detailed below. We would be really interested to hear your thoughts on this.

Best wishes
Stu

In their recent paper, Nowak et al. (hereafter "NTW") argue that inclusive fitness theory has been of little value in explaining the natural world, and that it has led to negligible progress in explaining the evolution of eusociality. However, their arguments are based on a fundamental misunderstanding of evolutionary theory, a misrepresentation of the empirical literature and a model that fails to offer any new insight. Here, we focus on three general issues regarding inclusive fitness theory.

First, NTW claim that there is a sharp distinction between the theories of inclusive fitness and natural selection. This is wrong. Inclusive fitness theory was not developed as an alternative to "standard natural selection theory", but rather to elucidate the ultimate function of Darwinian adaptation[1,2]. Consequently, rather than being an alternative, inclusive fitness theory is a proper expansion of natural selection theory, using population genetics to study behaviours that affect the Darwinian fitness of other organisms in addition to the actor[3]. For this reason, it is not surprising that the inclusive fitness theory generates predictions that are identical to those of "standard" natural selection theory[4,5]. Inclusive fitness theory is used to make falsifiable predictions about how natural selection shapes phenotypes.

Second, NTW suggest that Hamilton's rule requires a number of "stringent assumptions" such as pairwise interactions, weak selection, additivity and special population structures. However, we have long known that this is not the case. Hamilton's original formulations did not make all these assumptions, and generalisations based upon the Price equation have shown that none of them are required[2,4-6]. Hamilton's rule is as general as the genetical theory of natural selection itself. It is simply a partition of natural selection into its direct and indirect components. NTW's error is to have confused the completely general theory with models of specific cases, which do often make limiting assumptions for reasons of analytical or empirical tractability[4,7,8]. This

issue is well appreciated[6,9], and has not limited the power or precision with which inclusive fitness theory explains eusociality and predicts social interactions in real populations[10].

Third, NTW claim that inclusive fitness theory "does not provide any additional biological insight". They argue that it has delivered only "hypothetical explanations", leading only to "routine" measurements and "correlative studies", and that the theory has "evolved into an abstract enterprise on its own", with a "failure to consider multiple competing hypotheses". This claim is puzzling, for it completely neglects the extensive biological literature that has accumulated over the past 40 years in the fields of behavioural and evolutionary ecology. And this literature shows clearly that inclusive fitness theory has been vitally important in understanding behavioural phenomena such as sex allocation, policing, conflict resolution, cooperation, altruism, spite, kin discrimination, parasite virulence, parent-offspring conflict, sibling conflict, selfish genetic elements, cannibalism, dispersal, alarm calls, and genomic imprinting.

We do not have space to detail all the advances that have been made in these areas. However, the absurdity of NTW's claims is easily demonstrated with a single example, that of sex allocation (the ratio of investment into males versus females). We choose sex allocation because it is an easily quantified social trait, which inclusive fitness theory predicts can be influenced by interactions between relatives. While NTW argue that inclusive theory theory has provided only "hypothetical explanations" in this field, recent reviews of sex allocation show that the theory has provided strong explanation for why sex allocation varies with variables such as female density, inbreeding rate, dispersal rate, brood size, order of oviposition, sibmating, asymmetrical larval competition, mortality rate, the presence of helpers, resource availability and nest density in organisms such as protozoan parasites, worms, insects, spiders, mites, reptiles, birds, mammals and plants[4,11,12]. The quantitative success of this research can be summarized in one statistic: the percentage of the variance in the data explained by inclusive fitness theory has been as high as 96% in across-species studies and 66% in within-species studies (to put this in context, the average for evolutionary and ecological studies is 5.4%)[12,13]. In addition, as well as explaining adaptive variation in behaviour, inclusive fitness theory has even elucidated when and why individuals make mistakes (maladaptation)[14,15]. It is not clear how NTW can characterize such ringing success as "meagre".

Finally, the same points can be made with regard to the evolution of eusocial insects, which NTW see as a subject that inclusive fitness cannot explain. Haplodiploidy itself may have only a relatively minor bearing on the evolution of eusociality, but by impugning the value of inclusive fitness theory as well, Nowak et al. discard the baby with the bathwater. Inclusive fitness theory has explained why eusociality has evolved only in monogamous lineages, and why it is correlated with certain ecological conditions, such as extended parental care and defence of a shared resource[16,17]. Furthermore, inclusive fitness theory has made very successful predictions about behaviour in eusocial insects. It explains how worker egg laying varies with policing by other workers, how policing varies with relatedness, how workers respond to experimentally altered costs and benefits, why workers strive for more female-biased sex ratios, why sex ratios vary across colonies, how many individuals try to become reproductive, why workers sometimes kill queens, and why non-kin are actively excluded[16-18].

In all of these areas, the success of inclusive fitness theory derives from its ability to make testable predictions based upon measurable parameters, such as relatedness, promiscuity, effectiveness of policing or mortality rates. Our aim here is not to argue that inclusive fitness is the only way to model evolution, but to point out that it has already proven a productive and useful approach for studying eusociality and other social behaviours. In contrast, NTW's model provides no novel predictions and explains nothing that hasn't already been explained by existing theory. Their model merely confirms, in a less general way, Hamilton's original and immensely important point: if the ecological benefits are great enough, then altruism can be favoured between relatives.

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